Cyrilla racemiflora L. Swamp cyrilla

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Cyrillaceae Cyrilla family

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Cyrilla racemiflora L., called swamp cyrilla or leatherwood in the United States and palo colorado in Puerto Rico, grows in a variety of soils in both temperate and tropical regions extending from southeastern Virginia to northern Brazil. Probably best known as an ornamental bush or small tree in the Southeastern United States, swamp cyrilla reaches its maximum in both size and age in the montane forests of the West Indies. In the Luquillo Experimental Forest (LEF) of northeastern Puerto Rico, swamp cyrilla is the preferred nesting tree for the endangered Puerto Rican parrot, *Amazona vittata*.

HABITAT

Native Range

Swamp cyrilla grows naturally from 37° N. latitude in southeastern Virginia to 2° S. latitude in northern Brazil (*3, 39, 60*) (fig. 1). Swamp cyrilla has been observed in Central America, in the montane forests of the Greater and Lesser Antilles, in eastern Colombia, Venezuela, Guyana, and in northern Brazil. It has been reported as hardy as far north as New York and Massachusetts (*61, 66*).

More specifically, swamp cyrilla has been recorded in the Oaxaca region of Mexico (*60*), in central Belize, in the Caribbean coastal areas of northeastern Nicaragua (*37*), and in Panama (*33*). Swamp cyrilla is very common throughout Cuba and on the Isle of Pines (*2*). It is particularly common in pine forests and swamp areas where it occurs as a shrub (*50*). In Cuba's Sierra Maestra, it grows into a large tree. In Jamaica, swamp cyrilla is common as a shrub or small tree in the eastern parishes but is found only occasionally in the central parishes (*1*). In montane thickets and woodlands from 450 to 1,900 m in elevation, it grows into a large tree. Swamp cyrilla is also common in thickets and forests throughout Hispaniola (*6, 36*). Swamp cyrilla grows at elevations above 300 m in Puerto Rico's montane forests, which include Toro Negro, Maricao, Carite, and the LEF (*11, 39*). In the LEF, swamp cyrilla may grow to 1 m or more in diameter (*75*).

Swamp cyrilla is a component of the montane forests in the Lesser Antilles including Guadeloupe, Martinique (*7, 8, 23*), Dominica (*8*), and St. Vincent (*8, 82*), attaining large diameters in many instances. It is a common bush or tree in southern Venezuela (*54, 71*), in the Guyanan region of eastern Colombia (*25*), and in Guyana (*66*). Swamp cyrilla also grows in the watersheds of the Nhamunda and Trombetas Rivers northwest of Santarem, in the watersheds of the Negro and Curicuriari Rivers just south of the Equator in northwestern Brazil (*3*), and in the Serra de Araca of northern Brazil (*48*).

Swamp cyrilla's presence in the montane forests of the LEF, and presumably elsewhere in the Caribbean Basin, has spanned considerable time. Swamp cyrilla pollen grains, oblate spheroidal in shape, were among the more predominant grains encountered in LEF sphagnum bog profiles to depths approaching 80 cm (*45*).

Climate

The extreme northern range of swamp cyrilla in southeastern Virginia has mean monthly temperatures ranging from 5 °C during the winter to 26 °C in the summer (*42*). Annual rainfall averages 1150 mm. Frosts are not uncommon and may occur from November through late March. In southeastern Texas, mean annual rainfall varies between 1220 and 1420 mm, with mean annual temperatures near 20 °C (*43*). In the vicinity of Oaxaca, Mexico, swamp cyrilla grows in subtropical moist forests with a mean annual rainfall of about 1000 mm and a mean annual temperature of 20 °C (*51*).

In Central America, swamp cyrilla grows in subtropical moist forests in Belize, where mean annual rainfall is between 1500 and 2000 mm (*55*). It also occurs in the sub-

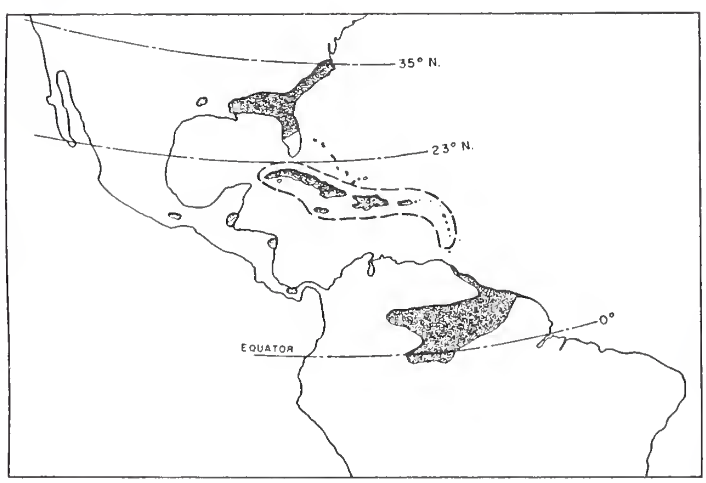

Figure 1.— *Shaded areas and areas within dashed lines indicate the range of swamp cyrilla (*Cyrilla racemiflora *L.) in the New World.*

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tropical wet forest of northeastern Nicaragua where the mean annual rainfall varies between 2000 and 3000 mm.

In the Caribbean Basin, swamp cyrilla is found in several of Holdridge's (*32*) life zones: subtropical dry, subtropical moist, subtropical wet, subtropical rain, lower montane wet, and lower montane rain forests. In Cuba, mean annual rainfalls varies from 1500 mm on the Isle of Pines to more than 2000 mm in the eastern mountains (*55*). In Jamaica, annual rainfall varies from 1500 to more than 4000 mm. Swamp cyrilla is most common in Puerto Rico in the lower montane wet forest and subtropical rain forest (*22*) where mean annual rainfall varies from 2500 to more than 4000 mm. In the Lesser Antilles, swamp cyrilla is found mainly in the lower montane wet and lower montane rain forest life zones, with annual rainfall from 2000 to 4000 mm or more. For most of the range of swamp cyrilla in the Caribbean Basin, mean annual rainfall varies from 1500 to 4000 mm, and mean annual temperatures range from 18 to 24 °C.

In northern South America (east-central Colombia, Venezuela, and Guyana), an area occupied mainly by tropical moist forests, mean annual rainfall varies from 2000 to 3800 mm (*55*). In Brazil, swamp cyrilla grows in tropical moist forests with mean annual rainfall of 2000 to 2800 mm and mean annual temperatures ranging from 24 to 26 °C.

Soils and Topography

Swamp cyrilla grows in various topographic positions and soils throughout its range. In the southeastern Coastal Plain of the United States, it grows as a shrub or small tree in shrub-dominated wetlands located in flat interstream uplands (pocosin wetlands) (*12, 49*). These areas are characterized by temporary surface water, periodic burning, and acidic soils of sandy humus, muck, or peat. Swamp cyrilla occurs in both low pocosins, the most nutrient-limited sites with deep peats, such as those occurring at the centers of bog complexes, and high pocosins, which occur on shallower peats (*12*).

In the Okefenokee Swamp of southern Georgia and northern Florida, swamp cyrilla grows on newly formed islands composed of peat and litter after having been initially colonized by sedges and grasses (*15, 26*). Throughout northern Florida, swamp cyrilla inhabits river banks, alluvial and nonalluvial swamps, and bay shores (*35*). Along the gulf coast, it grows in shaded river bottoms; on the borders of sandy swamps, near shallow ponds; and on high, sandy, exposed ridges rising above streams (*53*). It appears to grow well in sandy soil containing abundant moisture and organic matter (*61*).

In Cuba's montane forests, swamp cyrilla grows predominantly in acid clay soils (*10*). In Jamaica's montane forests, swamp cyrilla grows on exposed windward slopes (*57*). More recent investigations identify swamp cyrilla in the Blue, John Crow, and Port Royal Mountains, growing in four different conditions distinguished by topography and soils (*27, 63*). Wet slope soils are Lithosols, or thin soils over bedrock, with pH values ranging from 4.0 to 5.5. Mull ridge soils are deeper, more mature, and have a distinct accumulation of humus in the top 10 cm. Soil pH values are between 3.5 and 4.0. Mor ridge soils, on the knolls of ridges, have a deep humus layer and pH values varying from 2.8 to 3.8. Gully soils, also deeper with a discontinuous litter layer, have humus enrichment only within 3 cm of the surface. Their pH values range between 4.4 and 5.0.

In Puerto Rico, swamp cyrilla is common on ridges (*79*) and on gentle to moderate slopes at higher elevations in the LEF (*14*). Puerto Rico's soils are also acid clays, usually saturated, and sometimes shallow in depth over hardpans (*14*). Swamp cyrilla has also been reported on recent landslides with less organic matter and lower nutrient concentrations than those found in mature soils (*28*). In the Guyanan region of eastern Colombia, swamp cyrilla grows on windswept slopes at middle elevations, especially on poor sandy soils (*25*).

Decomposition studies of 65 freshly fallen swamp cyrilla leaves in Jamaica showed that 32 percent of the initial dry weight was lost after 1 year (*64*). Values for 14 other species in the same experiment ranged from 27 through ≥96 percent, suggesting that swamp cyrilla leaves decompose more slowly than those of most montane forest species.

Associated Forest Cover

Swamp cyrilla's extensive range in the New World, including both temperate and tropical forests, makes it a regular component of several different forest types. In the Southeastern United States, swamp cyrilla grows as a shrub or small tree in forests dominated by *Pinus echinata* Mill., *P. elliottii* Engelm., *P. palustris* Mill., and *P. taeda* L. (*5, 53*). *Acer rubrum* L., *Liquidambar styraciflua* L., *Nyssa sylvatica* Marsh., *Ulmus alata* Michx., and species of *Carya* and *Quercus* all occur as common hardwood associates in some part of the region. Along the Atlantic coast, swamp cyrilla grows with evergreen shrubs in interior swamps and upland bogs.

In Mexico and Central America, swamp cyrilla grows in both subtropical moist and subtropical wet forests. In Cuba, it grows as a small tree in the subtropical dry forest located in western Cuba and as a large tree in subtropical wet forests elsewhere on the island (*10*). In the remainder of the Caribbean Islands, swamp cyrilla is found in subtropical moist, subtropical wet, lower montane wet, and occasionally in lower montane rain forests. In South America, it grows mainly in tropical moist forests. Table 1 lists common tree associates for selected sites where species were enumerated.

LIFE HISTORY

Reproduction and Early Growth

Flowering and Fruiting.—The numerous small, white, five-part flowers are borne in flower clusters (spikelike racemes) about 7 to 14 cm long and slightly more than 1 cm broad (*39*). Clusters, ranging from 1 to 10, grow on twigs below most of the leaves. Individual flowers are about 0.5 cm across and have five pointed sepals; five pointed petals about 0.3 cm long, sometimes tinged with pink; five stamens; and a pistil with a two-celled ovary, short style, and two stigmas. Fruits are numerous, small, dry, and egg shaped (drupes) averaging 0.3 cm across. They are pink to red and contain two or three seeds.

Table 1.— *Major tree species associated with swamp cyrilla (*Cyrilla racemiflora *L.)*

Country or U.S. State	Locality	Elevation	Rainfall	Principal associated species	Source
		---- *m* ----	--- *mm/yr* ---		
Puerto Rico	Luquillo Mountains, subtropical wet and rain forests	350–600	2500–3800	*Dacryodes excelsa* *Euterpe globosa* *Micropholis garciniaefolia* *Sloanea berteriana*	(*14, 73, 74*)
	Luquillo Mountains, lower montane wet and rain forests	600–900	3000–4500	*Calycogonium squamulosum* *E. globosa* *M. chrysophylloides* *M. garciniaefolia*	(*23, 73, 74, 79, 84*)
	Cordillera Central, lower montane wet forest	>1000	~2500	*C. squamulosum* *Clusia grisebachiana* *M. chrysophylloides* *Prestoea montana*	(*9*)
Cuba	Pico Turquino, alpine thicket	1,800–2,000	1350	*Nectandra reticularis* *Ocotea foeniculacea* *Persea anomala* *Ternstroemia parviflora*	(*56*)
Jamaica	John Crow Mountains, lower montane rain forest	550	>2500	*Calophyllum globulifera* *Ficus suffocans* *N. antillana* *Psidium montanum*	(*4*)
	Blue Mountains, montane rain forest	750–1,200	>3500	*Clethra occidentalis* *Clusia rosea* *Coccoloba laurifolia* *N. patens*	(*4*)
	Blue Mountains, dwarf forest	>1,400	>4000	*Alchornea latifolia* *Brunellia comocladifolia* *Clethra occidentalis* *Podocarpus urbanii*	(*4, 57*)
	Blue, John Crow, and Port Royal Mountains, in gully, mor ridge, mull ridge, and wet slope forest types	>1,300	2500	*A. latifolia* *C. occidentalis* *Ilex macfadyenii* *P. urbanii*	(*27, 63*)
Dominica	Montane thicket	550	~4000	*Amanoa caribaea* *D. excelsa* *Licania ternatensis* *Oxythece pallida*	(*8*)
	Elfin woodland	>1,400	~5000	*Charianthus corymbosus* *Clusia venosa* *Didymopanax attenuatum* *Weinmannia pinnata*	(*8*)
Guadeloupe	Elfin woodland	—*	—*	*Clusia venosa* *Freziera undulata* *Myrcia microcarpa* *Richeria grandi*	(*8*)
United States	SE Atlantic Coastal Plain, Carolina bays	Near sea level	~1300	*I. coriaceae* *I. glabra* *Magnolia virginiana*	(*31*)

Table 1.— *Major tree species associated with swamp cyrilla (*Cyrilla racemiflora *L.) (continued)*

Country or U.S. State	Locality	Elevation	Rainfall	Principal associated species	Source
		---- *m* ----	--- *mm/yr* ---		
	SE Atlantic Coastal Plain, swamp forest	Near sea level	~1300	*Nyssa aquatica* *N. sylvatica* *Taxodium ascendens* *T. distichum*	*(12)*
North Carolina	Pocosin swamps	≤50	1250	*I. glabra* *M. virginiana* *Persea borbonia* *Pinus serotina*	*(49)*
South Carolina	Bay forest stands	Near sea level	~1300	*Gordonia lasianthus* *N. sylvatica* var. *biflora* *Persea borbonia* *Pinus taeda*	*(12)*
Southern Georgia, northern Florida	Okefenokee Swamp	Near sea level	~1300	*Gordonia lasianthus* *I. cassine* *P. elliottii* *T. ascendens*	*(26)*
	Okefenokee Swamp, cypress bays	Near sea level	~1300	*Acer rubrum* *Nyssa* spp. *Pinus* sp. *T. ascendens*	*(31)*

*Not measured.

In the Southeastern United States, swamp cyrilla blooms in June or July *(61)*. In Puerto Rico, flowering occurs during most of the year *(39)* with peaks in March and June *(21)*. Fruiting also occurs throughout the year *(39)* but with greater occurrence from August through December *(21)*. Fruit fall is mainly from October through December.

Seed Production and Dissemination.—Although swamp cyrilla produces abundant flowers and fruits each year, it rarely produces fertile seeds *(63, 66)*. Several attempts were made to collect seeds in Puerto Rico during the compilation of this report; none of these were successful.

Occasionally, a few trees are found that produce a greater number of fertile seeds. These trees are in areas where two different individuals are growing in close proximity *(66)*. Apparently, self-pollination of different flowers within the same clone will stimulate the formation of fruit, but actual fertilization of the ovule is achieved only by pollen from a different individual *(66)*. Available evidence suggests that swamp cyrilla trees are not self-compatible.

Swamp cyrilla seeds are small in comparison to the seeds of other canopy trees in the montane forests of Puerto Rico *(80)*. The Puerto Rican parrot (*Amazona vittata*), the pearly-eyed thrasher (*Margarops fuscatus*), and the Puerto Rican bullfinch (*Loxigilla portoricensis*) have all been observed eating swamp cyrilla fruits.[1] In addition to these bird species, the stripe-headed tanager (*Spindalis zena*), the Puerto Rican tanager (*Nesospingus speculiferus*), the red-legged thrush (*Turdus plumbeus*), and the scaly-naped pigeon (*Columba squamosa*) as well as a bat species, probably the Jamaican fruit-eating bat (*Artibius jamicensis*), have been seen feeding on swamp cyrilla fruits.[2] Other bird species and bats may also consume the fruits and distribute seeds.

Seedling Development.—Germination of swamp cyrilla seeds is hypogeal but has been further distinguished as phanerocotylar (the cotyledons escape the testa after germination) *(19)*. In the United States, swamp cyrilla commonly regenerates as an invader shrub in wet areas along roadsides *(66)*. After Hurricane Hugo in Puerto Rico, seedlings in the LEF were recorded in cleared areas adjacent to roads and on overturned root masses. Seedlings in closed forests, however, are rare *(80)*.

Vegetative Reproduction.—Swamp cyrilla propagates and spreads by vegetative shoots that arise from underground roots *(33, 66)*. It also sprouts vigorously after burning in pocosin ecosystems in North Carolina *(49)*. In the cool, moist environment of Puerto Rico's LEF, recumbent stems commonly send up new shoots *(59)*.

Swamp cyrilla is reported to be clonal and self-sterile within the clones in North American wetlands and lowland

[1]Arendt, Wayne. 1995. Personal communication with Wayne Arendt, wildlife biologist, USDA Forest Service, International Institute of Tropical Forestry, Call Box 25000, Río Piedras, PR 00928.

[2] Wiley, James. 1995. Personal communication with James Wiley, wildlife biologist, U.S. Fish & Wildlife Service, Grambling Cooperative Wildlife Project, Grambling State University, P.O. Box 4290, Grambling, LA 71245.

Cuba (*66*). Swamp cyrilla trees grow scattered throughout the wet, montane forests of Jamaica and Puerto Rico and do not appear to form clonal stands (*63*).

Sapling and Pole Stage to Maturity

Growth and Yield.—Swamp cyrilla is deciduous in colder regions (*61*) but evergreen in moist tropical forests (*39*). In North Carolina, swamp cyrilla loses its leaves gradually through the winter months (*49*). In contrast, leaf fall occurs throughout the year in Puerto Rico, with a maximum fall from April through July (*21*).

Swamp cyrilla produces growth rings in the temperate zone, but in the Tropics, the rings are obscure (*66*). In Puerto Rico, growth rings were reported for swamp cyrilla, but it was uncertain if the rings were annual (*68*). Current research on the phenology of swamp cyrilla in the LEF has shown that large-diameter earlywood vessels form in March, and smaller diameter latewood vessels form between October and November (*17*). If the rings are consistently formed on an annual basis at all sites within the forest, tree growth rates and age might be determined by extracting increment cores as in the Temperate Zone.

Without annual rings, estimates of growth rates and age must be done by recurrent measurement of the same stems. Diameter increment in the smallest d.b.h. classes (e.g., 4.1 to 20.0 cm) appears more rapid than in larger d.b.h. classes, particularly when stands have been disturbed or thinned (fig. 2).

The apparent slow growth of even-dominant swamp cyrilla stems in virgin stands suggested to early investigators that some trees could be quite old (*70*). The first age estimates for swamp cyrilla were made by determining the mean d.b.h. increment in select d.b.h. classes and then summing the periods required for the mean tree to pass through the d.b.h. class. Swamp cyrilla trees at 50 cm were estimated to be 700 years old, and those at 90 cm, to be 1,200 years old (*69*). Using the same methodology, the LEF's largest swamp cyrilla trees with a d.b.h. of 2.5 m would be about 3,600 years old! By comparison, the largest swamp cyrilla reported for the United States in Washington County, Florida, is only 37 cm in d.b.h. (*29*).

Another approach, disregarding the slowest growing trees (fig. 2) as unlikely to survive to the next d.b.h. class (e.g., trees growing at less than the mean d.b.h. increment in each d.b.h. class), yielded an estimate of 660 years of age for a 1-m swamp cyrilla (fig. 3). Moreover, it was noted that swamp cyrilla stems sometimes grew in close proximity, and the largest trees were very likely the result of proximate trunks fusing to form a single large stem (fig. 4a, b). It is unlikely, therefore, that the largest swamp cyrillas in the LEF exceed 1,000 years of age (*75*).

Swamp cyrilla leaf size varies considerably throughout its range (*66*). In the Blue Mountains of Jamaica, swamp cyrilla leaf anatomy was studied in detail (*65*). Specific leaf area averaged 54 cm^2/g, closely approximating 56.2 cm^2/g measured in the Luquillo Mountains of Puerto Rico (*83*). Lamina thickness, outer-wall thickness of the epidermis including the cuticle, the thickness of the palisade and nonpalisade layers, the presence of sclerenchyma and transcurrent sclerenchyma, stomate density, and mean guard cell length were also reported (*65*). In Puerto Rico's LEF, lower epidermis stomate numbers and pore sizes for swamp cyrilla were reported (*13*).

Six trees ranging from 9.8 to 30.7 cm in d.b.h. were sampled for biomass in the LEF (*46, 77*) (table 2). A regression equation,

$$Y = 0.031\,X - 5.96,\ r^2 = 0.98$$

developed for total biomass (Y in kilograms) as a function of X (d.b.h. in centimeters, squared, multiplied by height, in meters), was highly significant.

Chemical data for swamp cyrilla are shown in table 3. Swamp cyrilla growing in a riparian palm forest in the LEF had phosphorus concentrations (in mg/g) of 0.520 in leaves, 0.765 in branches, and 0.025 in trunks (*24*).

Rooting Habit.—Swamp cyrilla roots are shallow, densely matted, and without a taproot (*61, 66*). The major

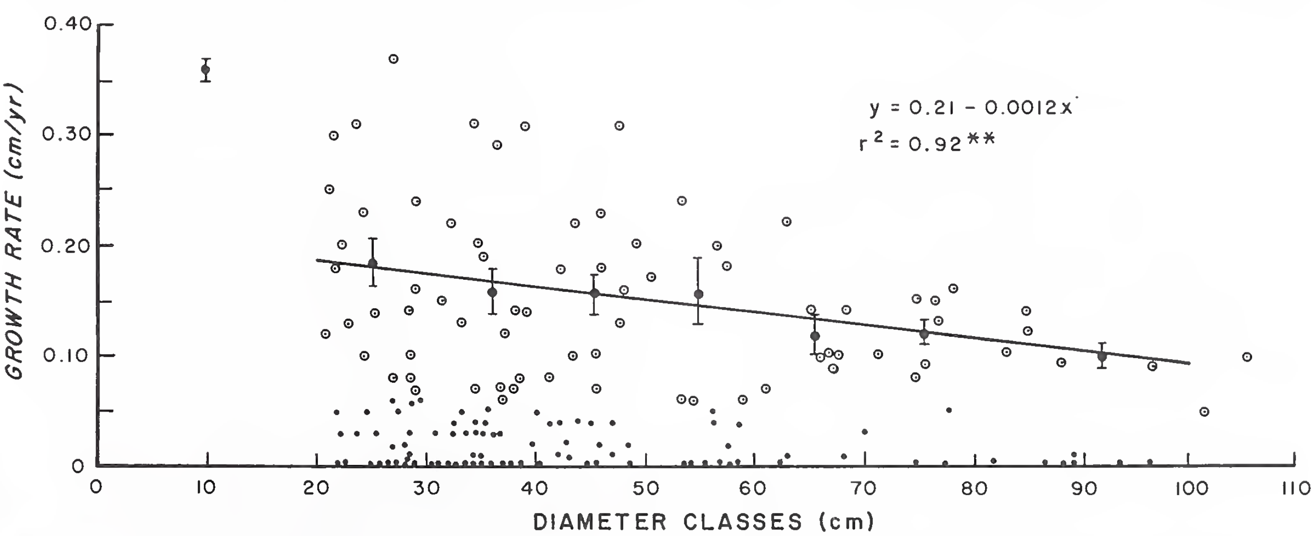

Figure 2.— *Scatter of points for diameter growth of swamp cyrilla (*Cyrilla racemiflora *L.) by diameter classes. Circled points are those used in the weighted least squares regression. Points with standard error bars represent the means and standard errors for the circled points within the respective diameter classes. The mean and standard error at 10 cm is for the ingrowth on the thinned plot. Solid dots indicate the growth rates that were discarded in the calculations of tree age.*

Table 2.— *Biomass data for swamp cyrilla* (Cyrilla racemiflora *L.)**

Tree dimension		Dry–weight biomass			
D.b.h.	Height	Leaves	Branches	Trunk	Total
- cm -	*-- m --*	*kg*			
9.8	9.1	0.61	9.65	13.03	23.29
12.8	10.1	2.77	22.90	32.25	57.92
15.2	9.6	0.28	19.85	30.49	50.62
20.8	12.0	4.96	50.47	121.94	177.37
23.4	11.7	4.11	73.44	77.55	155.10
30.7	13.4	10.27	163.00	218.11	391.38

*Sources: *46, 77.*

roots bend abruptly a few centimeters below the ground surface and run horizontally. Smaller branch roots, fibrous in texture, run both horizontally and vertically into the soil (*66*). Numerous adventitious shoots arise along the horizontal roots forming large vegetative clones in North American wetlands (*66*). Aerial roots are occasionally seen in the LEF descending from the base of trunks (fig. 4c), some hollow to the ground (fig. 4d). No mycorrhizal associations were detected on swamp cyrilla roots in the LEF (*20*).

Early nursery research demonstrated that cuttings would root but only to a limited extent and slowly (*61*). However, cutting during the growth stage in a humid environment using synthethic growth substances (e.g., indolebutyric acid, naphthaleneacetic acid, naphthaleneacetamide, or isoprene ester of naphthaleneacetic acid) in talc produces heavy rooting in 2 months.

Reaction to Competition.—Swamp cyrilla in the Southern United States grows well in full sun but was also reported to tolerate considerable shade (*61*). In the Okefenokee Swamp, swamp cyrilla was among the first woody species to invade newly formed peat islands within 3 to 6 years after the commencement of plant succession (*18*). It also recolonizes rapidly after fire disturbance (*16*).

In Puerto Rico, about 330 swamp cyrilla stems ≥4.1 cm occurring on several of the LEF's permanent plots were classified by crown class (*75*). Of these, 78 percent were dominant and codominant, 16 percent were intermediate, and only 6 percent were suppressed. The majority of swamp cyrilla, therefore, survive in conditions with direct exposure to sunlight.

Swamp cyrilla's large size and longevity in Puerto Rico led to its initial classification as a primary species. More detailed observations of its reproduction, early growth, and response to either natural disturbance or human intervention, however, indicate that swamp cyrilla is a long-lived component of the primary forest that exploits gaps during its regenerative phase (*62, 75*). In the LEF, it commonly grows into the dominant crown class regardless of elevation (*84*).

Swamp cyrilla's comparatively small seeds, its poor representation as either seedlings or understory trees in closed forests, and its relatively light wood indicate that it has more of the attributes of a secondary life cycle than a primary one (*58, 80*). In Jamaica, swamp cyrilla seedlings and saplings were absent on a 10- by 10-m plot containing eight mature swamp cyrilla trees (*63*). Swamp cyrilla was the only one out of 15 mature species sampled on the plot that did not have regeneration. However, following clearing of the plot, swamp cyrilla regeneration was observed in two separate cohorts (age classes) within 3 years (*62*). In Cuba, swamp cyrilla was observed rapidly colonizing a previously logged secondary forest on moist sites in mountainous terrain (*66*). Swamp cyrilla regeneration in the LEF has been observed in clearings, on landslides (*28*), and in previously thinned forests (*74*) but rarely in a closed forest (*58, 80*). Moreover, pole-sized swamp cyrilla trees are sometimes seen growing at a slight angle within closed forests in reaction to light entering through small gaps (*59*).

Curves showing d.b.h. class distributions for swamp cyrilla in natural stands of the LEF, one each for the 1946 and 1981 populations, are slightly different (fig. 5). In the 1946 distribution, the greatest proportion of stems was in

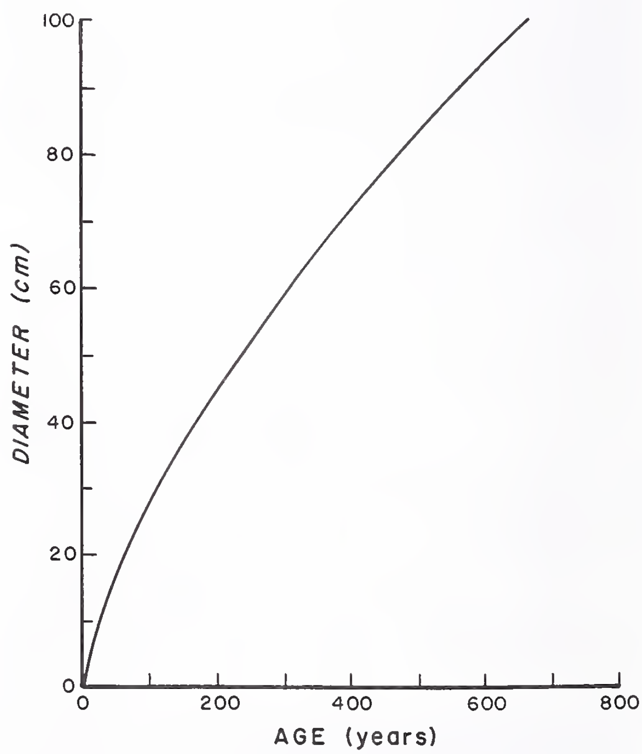

Figure 3.— *Age curve for swamp cyrilla* (Cyrilla racemiflora *L.).*

Figure 4.— *Composite of photos of swamp cyrilla (*Cyrilla racemiflora *L.) in the Luquillo Experimental Forest: A and B, examples of the coalescence of proximate stems forming a single, large trunk; C, aerial roots; D, large cavities.*

the 20- to 40-cm classes. In the 1981 distribution, the greatest proportion of stems was in the smallest d.b.h. class with a gradual decline of stems in the remaining classes. Both of these size-class distributions appear to be in response to previous hurricanes that passed directly over the LEF: the first, from hurricanes in 1766, 1772, and 1867; and the second, from a hurricane in 1932 (*75*). Moreover, about 3 years after the passage of Hurricane Hugo in 1989, swamp cyrilla regeneration was evident at a 650-m elevation in the LEF's Baño de Oro Natural Area (*81*). Scattered seedlings were seen growing on the ground in heavily disturbed areas as well as on the intact soil of root masses of wind-thrown trees.

In 1947, thinning of a 0.4-ha plot in a lower montane wet forest removed all canopy trees that were >50 cm in d.b.h., regardless of species (*74*). The thinning reduced the basal area by one-half, to 18 m^2/ha, and left all residual trees with at least 2 m of crown freedom. Tree crowns, many small and narrow, did not respond to additional light. No regeneration was observed 10 years later, and razor grass (*Scleria* sp.) had grown in gaps, making the prospects for natural regeneration appear unlikely.

About 30 years later, the previously thinned plot was assessed for long-term growth. By then, swamp cyrilla's stem numbers had increased 10 times, and its basal area also increased by 1.5 times in comparison to its initial composition before the thinning. In contrast, swamp cyrilla growing on seven control plots measured over the same period showed an 8-percent decline in stem numbers and a 44-percent loss of basal area (*74, 76, 78, 80*). This period of measurement on the control plots was characterized by an increase in forest biomass, a gradual closing of the forest canopy, and a decline in secondary forest species, all in response to the 1932 hurricane (*78*).

Damaging Agents.—At least 138 invertebrate species have been identified in swamp cyrilla wood during various stages of decay (*67*). Termites (*Parvitermes discolor* and *Glyptotermes pubescens*) and ants (*Pheidole moerens*, *Paratrechina* spp., and *Solenopsis* spp.) are the most abundant taxa. The wood of swamp cyrilla is also very susceptible to the dry-wood termite, *Cryptotermes brevis* (*41, 85*). The heartwood frequently rots in standing trees causing large cavities in the trunks and major branches (*59*) (fig. 4d).

Standing herbivory for 248 swamp cyrilla leaves sampled in the LEF was estimated at 5.4 percent of the total leaf area, but the herbivory rate determined for 51 leaves was only 0.12 percent per year (*83*). The amount of standing herbivory is somewhat low and is probably due to the low abundance of insects in the colorado forest (*59*). The rate value is very low and cannot be explained.

In the Southeastern United States, repeated fires, whether prescribed or wild, usually cause swamp cyrilla to recover in almost impenetrable thickets of small stems.[3] On experimental plots in the Okefenokee Swamp in Georgia, swamp cyrilla was heavily impacted by fires during the extreme drought of 1954 and 1955 (*16*). Within 2 years, swamp cyrilla had recovered and was among the most common species, maintaining its dense population through 1970.

SPECIAL USES

Swamp cyrilla heartwood has a very attractive, dark reddish-brown color; the somewhat lighter sapwood is not readily distinguishable from the heartwood (*40*). The wood has a fine and uniform texture, heavily interlocked grain,

[3] Balmer, William. 1995. Personal communication with William Balmer, U.S. Department of Agriculture, Forest Service (retired), Chamblee, GA 30341.

Table 3.— *Chemical data for swamp cyrilla (*Cyrilla racemiflora *L.)*

Component	Element						
	N	P	K	Na	Ca	Mg	Mn
	Percentage of dry weight						
Roots*							
Small	0.55	0.015	0.10	0.11	0.22	0.13	—†
Medium/large	0.12	0.003	0.05	0.14	0.25	0.06	—
Butt	0.22	0.010	0.21	—	0.46	0.05	—
Bole*	0.12	0.005	0.07	—	0.13	0.11	—
Branches*	0.26	0.023	0.19	—	0.20	0.07	—
Leaves*	0.83	0.035	0.26	—	0.23	0.12	—
Leaves‡	1.14	0.045	0.37	0.25	0.20	0.15	0.005
Leaves§							
Mor ridge forest	0.79	0.030	0.33	0.24	0.21	0.20	0.006
Mull ridge forest	1.02	0.020	0.49	0.16	0.36	0.11	0.006
Wet slope forest	0.89	0.020	0.37	0.27	0.33	0.18	0.016

*Luquillo Mountains, Puerto Rico (*46*).
†Not measured.
‡Blue, John Crow, and Port Royal Mountains, Jamaica (*27*). Also, Fe = 74, Zn = 19, and Cu = 2.0 p.p.m. in dry weight.
§Blue Mountains, Jamaica (*63*).

and moderate to low luster. Macroscopic features of the wood have been described (*3*).

Swamp cyrilla is relatively easy to saw, and the wood gives good results in all machining properties: planing and resistance to screw splitting are excellent; shaping, turning, boring, and mortising are good; and sanding is fair. Machined surfaces are glossy smooth with darker pieces having an oily feel. However, swamp cyrilla seasons slowly and undergoes severe degrade in the process: high shrinkage, severe warp, surface checking and splitting, casehardening, collapse, and honeycombing. Degrade is so severe that most air-dried lumber is unfit for commercial use (*40*). Because swamp cyrilla was an undesirable timber species, it was girdled during timber stand improvement activities in the LEF during the 1940's (*59, 72*). It was also frequently used for charcoal.

The wood is considered durable, although test data are lacking. Its most satisfactory use would be as green wood in submerged conditions such as buried pilings or underwater parts of docks and wharves where drying is impossible. The wood has a specific gravity of 0.53 g/cm^3 (*39, 44*) and contains tannins (*47*).

Swamp cyrilla, with its attractive white flowers (*30*) and foliage that turns to brilliant shades of orange and scarlet, is grown in Temperate Zone gardens as an ornamental (*53*). In the northernmost part of its range, the foliage is deciduous in the autumn or early winter; southward, in the United States, the foliage remains persistent with little change of color until the beginning of the following summer.

Swamp cyrilla was reported as a honey plant in the United States (*61*) even though most of the time it produces little nectar (*52*). During years of abundant nectar and pollen production, however, swamp cyrilla is responsible for a condition called "purple brood," which kills the brood of bees, turning the brood a rich purple color. In both Cuba (*39*) and Puerto Rico (*59*), swamp cyrilla's hollow trunks have supported bee populations.

The bark of swamp cyrilla is rich in phenolic compounds and has been used as a styptic or astringent (*66*). Another medicinal use of the bark is for treatment of wounds and ulcers with the intent of cicatrizing them.

In large trees, swamp cyrilla heartwood frequently rots causing cavities in the trunks and large stems. This characteristic makes swamp cyrilla the single most important species for nesting of the rare and endangered Puerto Rican parrot (*59*). Perhaps the most unique human use of a large swamp cyrilla tree was as a rain shelter by local inhabitants on the island of Dominica—small wooden stools and a plywood table were placed in the hollow of the 3-m-d.b.h. tree.

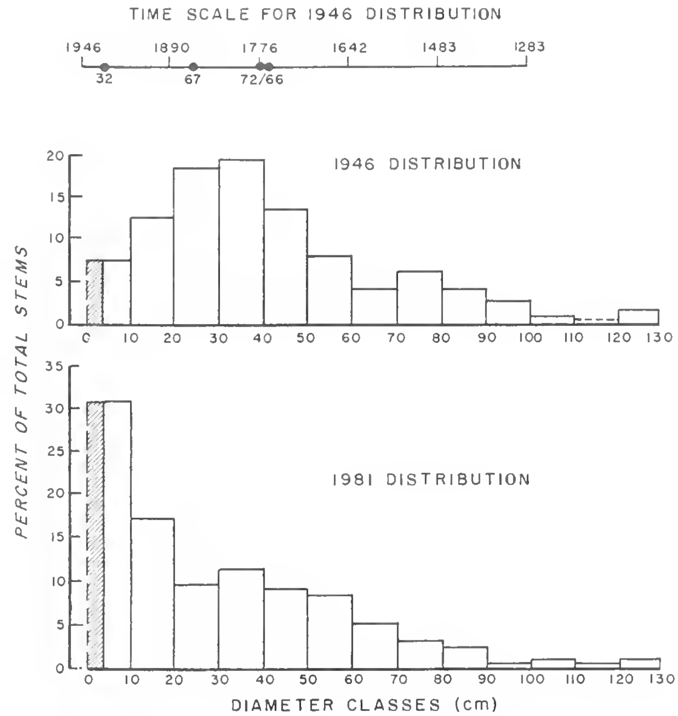

Figure 5.— *Diameter class distributions of swamp cyrilla (*Cyrilla racemiflora *L.) on undisturbed long-term plots within the colorado forest of the Luquillo Mountains in 1946 and 1981. The time scale indicates the years to which the diameter class corresponds according to the synthesized age curve (fig. 3) as well as the years that hurricanes passed directly over the Luquillo Mountains. The shaded portion of the smallest diameter class, that is <4.1 cm, was not tallied in the field.*

GENETICS

The family Cyrillaceae contains 3 genera and 14 species (*66*). The fossil record of the family indicates that it had representatives in North America since the Upper Cretaceous period. The genus *Cyrilla* is considered by some to be monotypic, whereas others have recognized as many as 10 species. Most authors dealing with phylogentic classifications involving the family have placed it with either the Ericales or the Celestrales.

Cyrilla racemiflora L. was originally described by Linnaeus in 1767 with material sent from South Carolina. A second species, *C. antillana* Michx., was described in 1803, apparently from material collected in the West Indies, but was later designated by Urban and Standley as *C. racemiflora* (*33, 60, 66*). A third species, *C. parvifolia* Raf., was described from the United States in 1840 (*66*). Found locally in swamps from Georgia to Florida as a low shrub with smaller leaves and shorter racemes, this purported species was reduced to a variety, *C. racemiflora* var. *parvifolia* Sarg. (*38, 53*). Other specific names (*66*) that have been assigned to the genus include: *C. arida* Small, from material collected in the southern lake region of Florida; *C. brevifolia* Brown, from material collected in Guyana, and *C. cubensis* Wilson, *C. nitidissima* Urban, and *C. nipensis* Urban, from different areas in Cuba. Eastern Cuba is the area with the greatest degree of local variation in swamp cyrilla (*66*).

Cyrilla racemiflora is extremely polymorphic. This is particularly apparent when extreme forms from different geographical regions are compared (*33, 66*). However, there are no gaps or discontinuities separating one genetic pattern from another. Instead, different patterns are connected by intermediate forms.

Swamp cyrilla's clonal reproduction is correlated with a high incidence of seedless parthenocarpy (the production of fruits in the absence of fertilization) in populations where self-pollination is likely. Sexual reproduction in these populations is minimal causing a pattern of variation in which

morphologically distinct populations occupy different environments (*66*).

The chromosome number reported for most cells in swamp cyrilla is 20, ranging from 18 to 22 (*66*). The nuclear volume of shoot apex cells was determined at 88.4 $\mu^3 \pm 13.4$ (*34*).

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